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Trogosus-like tillodont (Tillodontia, Mammalia) from the early Middle Eocene of Japan

KAZUNORI MIYATA and YUKIMITSU TOMIDA

Department of Environmental Science, Graduate School of Science and Technology, Kumamoto University, Kurokami-cho 2-39-1, Kumamoto 860-0862, Japan

Department of Geology, National Science Museum, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 169-0073, Japan

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Abstract. A trogosine tillodont, represented by seven fragmentary teeth, is described from the upper part of the Akasaki Formation, early Middle Eocene of Japan. The stratigraphic horizon of the new material is almost the same as that of the holotype of *Higotherium hypsodon*, which is the most recently described tillodont from Japan. In spite of poor preservation, the dental characters of the new specimens are distinguishable from those of the Asian trogosine genera including *Higotherium*, and they may be referable to *Trogosus*, which has been recorded only from the Bridgerian of North America. This *Trogosus*-like tillodont inhabited East Asia together with more advanced *Higotherium* during the early Middle Eocene.

Key words: Akasaki Formation, early Middle Eocene, *Higotherium*, Tillodontia, Trogosinae, *Trogosus*

Introduction

Recently, several new tillodonts have been found in Asia (e.g., Ting and Zheng, 1989; Chow *et al.*, 1996; Miyata and Tomida, 1998), and tillodont origin and dispersal have been discussed repeatedly based on various phylogenetic hypotheses (Stucky and Krishtalka, 1983; Baudry, 1992; Lucas, 1993; Chow *et al.*, 1996; Miyata and Tomida, 1998). The subfamily Trogosinae Gazin, 1953 is generally believed to be a monophyletic group, and includes five derived genera of Tillodontia: *Trogosus* Leidy, 1871, *Tillodon* Gazin, 1953, *Kuanchuanius* Chow, 1963a, *Chungchienia* Chow, 1963b (see also Chow *et al.*, 1996), and the recently erected genus *Higotherium* (Miyata and Tomida, 1998). Trogosine material from Asia is rare but provides significant records for understanding tillodont diversity during the Middle Eocene. North American trogosines, *Trogosus* and *Tillodon*, have been recorded only from the Bridgerian land mammal age (latest Early to early Middle Eocene; Prothero, 1995). *Kuanchuanius* and *Higotherium* are known from the early Middle Eocene of China and Japan, respectively, and *Chungchienia* is known from slightly younger Middle Eocene strata of China (Chow *et al.*, 1996). Considering the monophyly of Trogosinae, the appearances of these genera indicate that their divergence had already occurred prior to the Middle Eocene and continued well into the Middle Eocene.

Although our knowledge of Asian trogosines is limited to rare and incomplete material, the three Asian genera mentioned above are easily distinguishable from North American genera in having several derived dental characters. In comparison with North American taxa, trogosine diversity at the generic level is likely more advanced in Asia, and to date no genus has been recorded from both North America and Asia. *Kuanchuanius shantunensis* Chow, 1963a was regarded as the most closely related taxon to the North American genus *Trogosus* (Stucky and Krishtalka, 1983; Lucas, 1993), but this Asian species is distinct in having a peculiar I/2 morphology (Chow, 1963a; Miyata and Tomida, 1998).

Seven fragmentary teeth of the tillodont described here were found in the red siltstone belonging to the upper part of the Akasaki Formation, at Iwajima within Ohyanomachi, Kumamoto Prefecture, Japan (Figure 1). The stratigraphic horizon is placed approximately 2 m below the base of the Shiratake Formation, which conformably overlies the Akasaki Formation and bears marine molluscan fossiliferous horizons, namely Lower *Orthaulax* Zone of Nagao (1926), in the basal part. On the basis of our field investigation, the tillodont horizon is almost equal to that of the holotype of *Higotherium hypsodon*, thus the geological age is most likely the early Middle Eocene (see geological setting in Miyata and Tomida, 1998). Although a precise generic assignment of the new tillodont material is difficult because of the poor preservation, it apparently belongs to Trogosinae judging from the dental characters. Moreover, the tooth remains described here closely resemble those of *Trogosus* in morphology, but apparently differ from those of the three Asian genera mentioned above. In this paper, we provide evidence that a *Trogosus*-like tillodont inhabited East Asia during the early Middle Eocene.

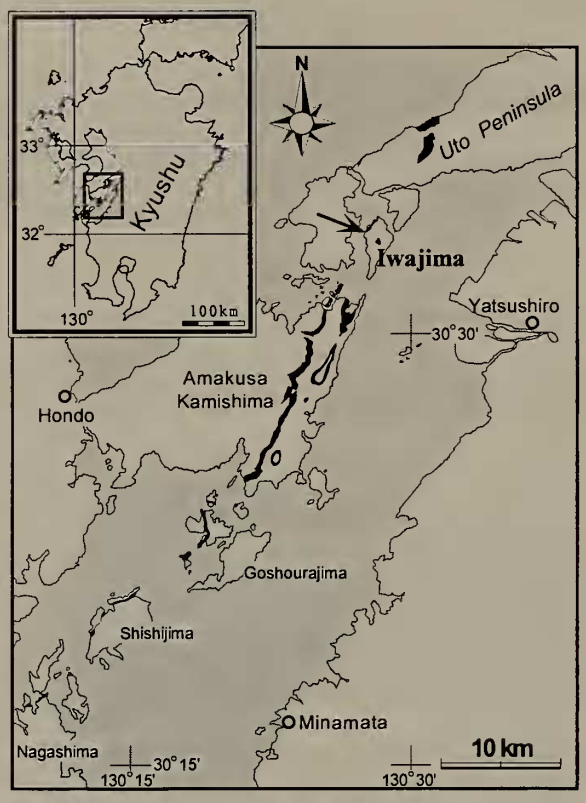

Figure 1. Map showing the fossil locality (allow), Iwajima in Ohyanomachi, western part of Kyushu, Japan, and the distribution of the Akasaki Formation (black area).

The following institutional abbreviations are used in this paper: **AMNH**, American Museum of Natural History, New York, New York, USA; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, People's Republic of China; **NSM**, Department of Geology, National Science Museum, Shinjuku, Tokyo, Japan; **USNM**, National Museum of Natural History, Washington, D.C., USA; **YPM**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Systematic paleontology

Order Tillodontia Marsh, 1875
Family Esthonychidae Cope, 1883
Subfamily Trogosinae Gazin, 1953
Genus ***Trogosus*** Leidy, 1871

Type species.—*Trogosus castoridens* Leidy, 1871

Cf. ***Trogosus*** sp.

Figures 2, 3

Material.—Seven fragmentary teeth, NSM-PV 20121: partly damaged right I/2 (Figures 2A, B), fragmentary left I/2 (Figure 2C), enamel remains of right and left I2/? (Figures 2D, E), cracked right P/4 (Figure 2F), trigonid portion of a right lower molar (Figure 2G), and broken talonid portion of right M/3 (Figures 2H-J).

Locality.—Western coast at Iwajima, Ohyanomachi, western part of Kumamoto Prefecture, Japan (Figure 1).

Horizon and Age.—Upper part of the Akasaki Formation, most likely early Middle Eocene (see also Miyata and Tomida, 1998).

Occurrence.—Seven fragmentary teeth (NSM-PV 20121) described below were found in two adjoined concretions from the red siltstone belonging to the Akasaki Formation. The cracked right P/4 and a trigonid portion of a right lower molar (Figures 2F, G) were found from the small concretion (approximately 12 cm in diameter), the other five fragmentary teeth were found from the large concretion (approximately 25 cm in diameter). These teeth are probably of a single individual judging from the massed occurrence.

Description.—All the teeth described below are poorly preserved, and in a few instances all that remains is enamel. However, based on our examination, they are identifiable as fragments of four elongated rootless teeth with enamel bands restricted to the anterior surfaces (second incisors, Figures 2A-E) and three rooted hypsodont teeth with columnar-shaped enamel walls (lower cheek teeth, Figures 2F-J). Illustrations of the reconstructed right I/2, P/4, and M/3 talonid are shown in Figure 3, and measurements of NSM-PV 20121 are presented in Table 1.

Second incisors: The four elongated fragments (Figures 2A-E) are remains of rootless teeth with restricted enamel covering; the enamel layer is distributed on the labial surface and the anterior part of the mesial and distal surfaces. In these fragmentary teeth their mesial and distal sides are distinguishable; the extension of enamel covering on the distal side is greater than on the mesial side, as seen in rodent incisors. Only one tooth (Figures 2A, B; 3A-C) barely retains its natural shape among the four elongated teeth and is certainly identifiable as the right I/2 of a trogosine tillodont. The right I/2 is 85 mm in length from its tip to the proximal end as preserved. It is curved in lateral view, and the tip is chisel-shaped. The labial and distal enamel surfaces of the right I/2 are nearly flattened and are ornamented with weak, longitudinal lines (rugose). Moreover, a growth line-like pattern is observable on the mesial surface of the enamel and is slightly curved toward the tip of the crown (Figure 3C). Both the labiodistal and labiomesial corners of the I/2 are rounded in cross section (Figure 3B). The enamel-free dentine of the right I/2 is partly disintegrated but apparently elongated posteriorly, and its distal side is in the same plane as the enamel covering part. Three other fragments lack dentine (Figures 2C-E) but possess similar enamel features to that of the right I/2. However, the three fragments are too incomplete to permit identification of their position in the jaw. Nevertheless, one of them (Figure 2C) is considered as a fragment of left I/2 because it was found close to the right I/2. The two remaining fragments (Figures 2D, E) were also found in the same concretion but were separated from the lower incisors when collected. These two enamel fragments (Figures 2D, E) are tentatively interpreted as parts of the right and left I2/, respectively, judging

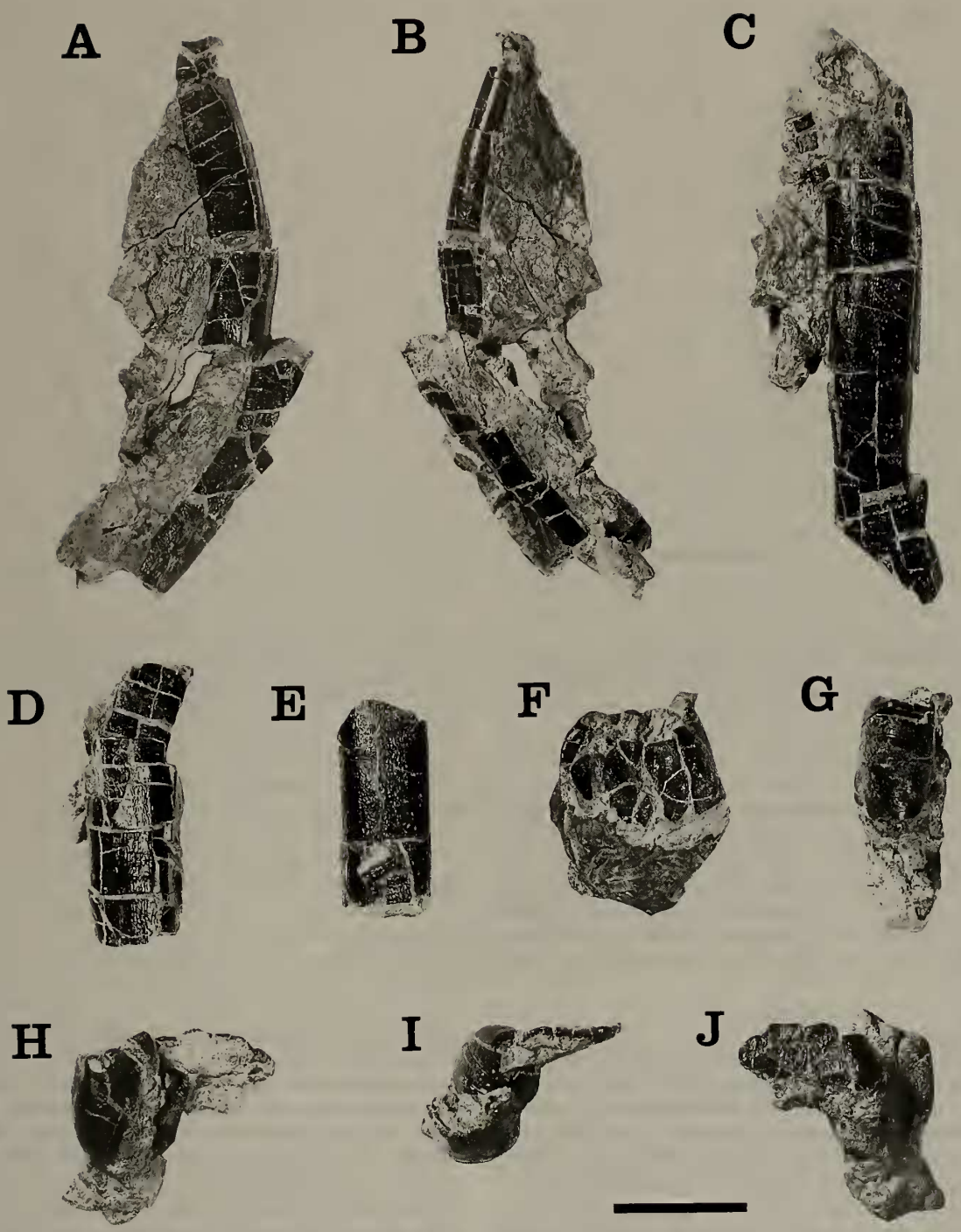

Figure 2. Cf. *Trogosus* sp., NSM-PV 20121. **A-B**: right I/2; A, distal view; B, mesial view. **C**: left I/2, labial view. **D**: right I2/?, labial view. **E**: left I2/?, labial view. **F**: right P/4, buccal view. **G**: trigonid portion of a right lower molar, buccal view. **H-J**: right M/3 talonid; H, buccal view; I, occlusal view; J, lingual view. Scale bar equals 2 cm long.

from the enamel development on the lateral sides and the curvature of the growth line-like pattern in the enamel.

Lower cheek teeth: The lower cheek teeth (Figures 2F-J) of NSM-PV 20121 are also incomplete and damaged, and the cusp pattern on the fragmentary teeth is obscured because of heavy wear and poor preservation.

The P/4 of NSM-PV 20121 (Figures 2F, 3D) is incompletely prepared; it is impossible to remove all of the matrix from

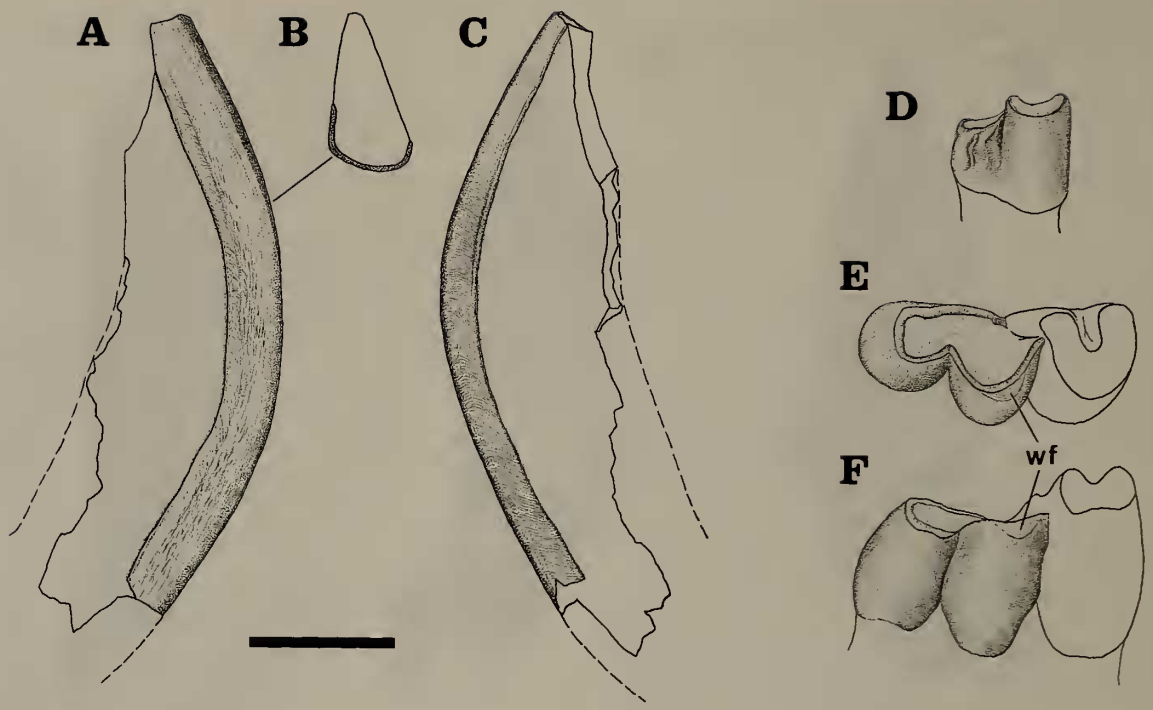

Figure 3. Sketches of reconstructed right I/2, P/4, and M/3 talonid of NSM-PV20121, cf. *Trogosus* sp. **A-C**: right I/2; A, distal view; B, cross section; C, mesial view. **D**: right P/4, buccal view. **E-F**: right M/3 talonid; E, occlusal view; F, buccal view. wf: a crescentic wear facet on the cristid obliqua. Scale bar equals 2 cm long.

Table 1. Measurements (in mm) of NSM-PV 20121, cf. *Trogosus* sp. Asterisks (*) indicate measurements of portions with damage.

Transverse width of right I/2	11.4
Anteroposterior length of right I/2	23.1
Transverse width of left I2/? (enamel portion)	13.3
Transverse width of right P/4 trigonid	15.5*
Transverse width of right M/3 talonid (second lobe)	16.2*
Transverse width of right M/3 third lobe	13.3

this specimen, but most of the crown portion is visible. Although the lingual portion of the tooth and the cristid obliqua are damaged, this tooth is identified as a bilobed hypsodont tooth; the buccal wall of the trigonid is columnar and is U-shaped in horizontal section. It is difficult to accurately measure the talonid owing to poor preservation, but it is somewhat shorter in width and length than the trigonid portion, judging from the enamel remains. The buccal wall of the hypoconid considerably inclines toward the occlusal surface, and the posterior wall of the talonid is relatively flattened. A small, longitudinal swelling of enamel occurs on the buccal wall anterior to the hypoconid (Figure 3D); a similar structure is rarely seen in other trogosine specimens.

The tooth fragment with the buccal enamel wall (Figure 2G) is tentatively considered the trigonid of a right lower molar; it apparently represents a rooted, hypsodont tooth, although its root and the lingual enamel wall are mostly missing. The columnar buccal wall is slightly convex in vertical section at the base of the crown.

The talonid portion of a right M/3 (Figures 2H-J) is broken; the second lobe was displaced posterobuccally relative to the third lobe (Figures 3E, F), and most of the root is also missing. The buccal enamel wall of the talonid is high and double-columnar, whereas the lingual enamel wall, which has a trace of the talonid notch, is low and almost flattened (Figures 2I, J). These enamel features of the M/3 talonid suggest that this tooth is hypsodont on the buccal side, in contrast to the enamel development on the lingual side, as in other trogosine molars. The buccal wall of the second lobe is swollen, V-shaped in horizontal section (Figures 2I, 3E) and is externally convex in vertical section. Although the cristid obliqua is cracked, a crescentic wear facet is present on the cristid obliqua near the occlusal surface (wf in Figures 3E, F); this wear facet on the cristid obliqua is also seen on other trogosine molars. The basin-shaped

third lobe is extremely elongated posteriorly, with a wear facet sloping to the buccal side, and the posterior wall of the third lobe is rounded in horizontal section.

Discussion

In spite of poor preservation, NSM-PV 20121 certainly belongs to the subfamily Trogosinae; fragments of rootless, elongated, gliriform teeth and the rooted hypsodont teeth are referable to the second incisors and lower cheek teeth of a trogosine tillodont, respectively. The possession of gliriform I2/2 and an elongated, basin-shaped third lobe of M/3 are diagnostic dental characters of Trogosinae (Gazin, 1953).

Schoch (1986) noted morphological similarities between the second incisors of trogosine tillodonts and the canines of stylinodontid taeniodonts, especially those of *Stylinodon* and *Ectoganus*. Thus, taxonomic assignment for such an isolated gliriform tooth has been confused in some previous studies (Schoch, 1986). However, the gliriform teeth described here are not as laterally compressed as in canines of stylinodontids; and as the right I/2 shows, the distal enamel surface is in the same plane as the posterior dentine (Figure 3B); these characters indicate that NSM-PV 20121 belongs to the Trogosinae. Moreover, lower molars of trogosines are readily distinguished from those of stylinodontid taeniodonts; in stylinodontid molars, trigonids and talonids are anteroposteriorly compressed (trigonid and talonid are no longer divided in lower molars of *Stylinodon*), plus the enamel layer distinctly extends into the alveolus on both buccal and lingual sides, the buccal crowns are not so convex in vertical section as in *Trogosus*, and the third lobe on M/3 is not elongated (Schoch, 1986; Chow *et al*., 1996). Although the cheek teeth of NSM-PV 20121 are incompletely preserved, they show no features of stylinodontid molars.

In comparison with previously known trogosines, NSM-PV 20121 closely resembles species of *Trogosus* in morphology. The right I/2 is nearly equal in size to those of *Trogosus* species, but its enamel extension on the distal side is relatively wider than that of the holotypes of *Trogosus grangeri* (AMNH 17008) and *Tillodon fodiens* (YPM 11087). The fragmentary lower cheek teeth (Figures 2F-J) are relatively large compared to those of *Trogosus* species; they are similar in size to those of the largest specimen of *T. grangeri* (YPM 16449) examined by Robinson (1966). Moreover, the degree of hypsodonty and the convexity of the buccal walls on the lower molars further are similarities to *Trogosus*. Compared with the best-preserved lower molars of *Tillodon fodiens* (USNM 18164, hypotype), the molars of NSM-PV 20121 are more hypsodont, and their crowns are less tapering upward.

On the other hand, NSM-PV 20121 described here is apparently distinguishable from species of *Kuanchuanius, Higotherium*, and *Chungchienia*. All the fragmentary teeth are considerably larger than those of the holotype of *K. shantunensis* (IVPP V 2764), in which the I/2 possesses a longitudinal shallow groove on its labial surface and anteroposteriorly shortened enamel-free dentine; the unique I/2 features of *K. shantunensis* are not seen in either NSM-PV 20121 or other trogosine specimens (Chow, 1963a; Miyata and Tomida, 1998). Incisors of *Higotherium* have been unknown to date, but NSM-PV 20121 apparently differs from *H. hypsodon* in having much less hypsodont lower molars and posteriorly elongated M/3 third lobe. Undoubtedly, NSM-PV 20121 differs from species of *Chungchienia*, in which all known teeth are far more highly specialized; the lower cheek teeth of *Chungchienia* are extremely hypsodont and rootless, with unilaterally distributed enamel layer (see figure 2 in Chow *et al*., 1996). Therefore, NSM-PV 20121 is readily distinguishable from the Asian taxa mentioned above, and it may be referable to the North American genus *Trogosus*.

In addition to *K. shantunensis*, Chow (1963a) described two fragmentary but significant I/2 of trogosines from China: "Tillodontia, gen. indet. sp. 1" (IVPP V 2765) and "Tillodontia, gen. indet. sp. 2" (IVPP V 2766). IVPP V 2765 and IVPP V 2766 are recorded from the Heti Formation in Yuanchu Basin and the Lushi Formation in Lushi Basin, respectively (Li and Ting, 1983); both formations are placed within the Middle Eocene (Tong, 1989; Prothero, 1995). The latter specimen (IVPP V 2766) was subsequently referred to "? *Stylinodon* sp." by Chow *et al*. (1973), but later Schoch (1986, p. 121) reidentified the specimen as a fragmentary I/2 of a trogosine tillodont. The right I/2 of NSM-PV 20121 is slightly larger than IVPP V 2765 and is apparently smaller than IVPP V 2766 judging from the illustrations of Chow (1963a). However, except for the size differences, the morphology of these two I/2 from China is basically similar to the North American taxa also. These two Chinese specimens apparently cannot be referred to species of *Chungchienia* in size and morphology, and we have no evidence that IVPP V 2765 and/or IVPP V 2766 are identifiable as I/2 of *Higotherium*. Nevertheless, the two I/2 fragments described by Chow also suggest that other undescribed or uncharacterized trogosines inhabited Asia during the Middle Eocene. The record of NSM-PV 20121 suggests that a *Trogosus*-like tillodont inhabited East Asia together with an advanced form (*Higotherium hypsodon*) during the early Middle Eocene. In addition, this new material strongly indicates the closest affinity with North American trogosines among all known Asian material.

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